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STUDY OF MONKEY, APE AND HUMAN MORPHOLOGY AND PHYSIOLOGY RELATING TO STRENGTH AND ENDURANCE

PHASE III

THE TESTING OF CHIMPANZEE STRENGTH PRIOR TO 1961

TECHNICAL DOCUMENTARY REPORT NO. ARL-TDR-63-22

July 1963

6571st Aeromedical Research Laboratory
Aerospace Medical Division
Air Force Systems Command
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(Prepared under Contract No. AF 29(600)-3466 by William E. Edwards, Contractor and Author, Columbia, S.C., and Chicago, Ill.)

FOREWORD

In 1958, the writer initiated a study of the strength of humans and other primates, including detailed consideration of the criteria for adequate strength testing. This study was continued from 1959 to 1961 at the University of Chicago as a National Science Foundation Science Faculty fellow.

With the interest and help of Lt. Col. Hamilton H. Blackshear, USAF, MC, and Maj. James Cook, USAF, VC, in 1961 extensive laboratory studies (to be published in 1963) were conducted at the 6571st Aeromedical Research Laboratory of Holloman Air Force Base, and the report was prepared the following year at the University of Chicago. The writer is also indebted to Maj. Robert H. Edwards of the Aeromedical Research Laboratory for his helpful encouragement in the study here reported.

ABSTRACT

Muscular strength as an area of significant functional differences between man and chimpanzee is probably second only to higher mental function. Anecdotal observations suggesting markedly superior strength in apes are confired by the studies of Baumen (1923; 1926). Motivated by rage and curiosity, adult chimpanzees pulled a handle attached to a rope, using one or both hands; dynamometer readings showed forces four and three times as great respectively as those produced by men of equivalent body-weight. In another experiment eight adult chimpanzees pulled a rope lacking a handle for increasing food incentives (Finch, 1943); their performances were only slightly superior to those of humans, body-weight considered. The contradictory findings are likely due to inadequate and inconsistent methodology, since neither experimental design satisfied more than a few of approximately thirty-seven essential criteria.

PUBLICATION REVIEW

This Technical Documentary Report has been reviewed and is approved for publication.

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THE TESTING OF CHIMPANZEE STRENGTH PRIOR TO 1961: METHODS AND RESULTS

1. INTRODUCTION

Many aspects of function as well as form are now fairly well known for a variety of animal species other than man. One of the most important functions in all higher animals is that of voluntary muscular contraction, but the magnitude of its force in non-human species is virtually unknown, for almost without exception such studies have been conducted by using artificial (electrical) stimulus, generally on excised muscle tissue in vitro. Yet it is essential to have comparative data on this aspect of animal physiology to understand the changes, associated with culture, in optimum levels of functioning; for example, humans may gain advantage from reduced ease of "firing" motor units and from reduced muscular force. Another likely unique factor operative in human evolution is the lowering of most selective pressures with the advent of enormously advantageous culture, which is thus compensatory of relatively slight biological defects.

For two factors, among all non-human species, the most suitable subject for such comparative strength tests is the chimpanzee. First, the chimpanzee can with the greatest rapidity learn to move or attempt to move a given portion of its body with maximal force; second, the variety of movements which it can be trained to perform is, consistent with the chimpanzee's largely arboreal primate nature, among the greatest of all species. Also, the body-size of the chimpanzee seems ideal for detailed, complex strength measurements which would be much more difficult with such small laboratory subjects as rats, which are unsuitable in any event because of their less varied muscle actions and their virtual inability to be trained to standardized performance with exertions of maximal force.

Strength studies of chimpanzees have a special significance to those concerned with the pure as well as with the applied science of human anatomy and physiology, for -- with the likely exception of gorillas and possible exception of gibbons -- chimpanzees provide the closest extant analogues to man in the greatest number of respects of bodily form and function (Schultz, 1936; Hooton, 1946, pp. 39-44). Such knowledge of chimpanzee strength is thus applicable to research involving the use of chimpanzees as analogues of humans -- as in the current man-in-space program -- for the differences between man and ape in strength appear to be the most marked major difference occurring, with the exception of those associated with higher mental functions.

Finally, muscular strength is a major determinant of behavior in every primate species, so knowledge of the strength of chimpanzees is highly significant to all research concerned with their physical, physiological, and psychological characteristics.

In at least partial recognition of the broad applicability of knowledge of chimpanzee strength to other areas of research, a great deal of interest in the strength of chimpanzees and other apes has long existed. But most accumulated data have been procured by mere chance observations, while that resulting from laboratory experimentation has not only been relatively limited quantitatively but markedly inconsistent in indicating the absolute strength of chimpanzees and that relative to man's.

In discussing a somewhat comparable and related area of research, Harlow (1951, p. 222) commented: "Possibly what is most needed to give new life to this old problem is a relatively novel approach by an investigator who is not thoroughly steeped in the knowledge of bygone failures." With the advantages of an independent approach in mind, the present writer attempted first to determine the criteria essential to an adequate program of experimental research on chimpanzee strength and then made detailed comparisons with and evaluations of previous research. For optimal explication, approximately the same sequence will be followed in this paper, with random observational data followed by consideration of adequate experimental research design; after a description of strength testing performed prior to the writer's laboratory research in 1961 is described, the research design criteria will be applied to an evaluation of earlier strength testing.

2. ANECDOTAL OBSERVATIONS

Purely accidental, or at least incidental, observations caused the chimpanzee in the earliest years of his formal study in the laboratory to become regarded as markedly superior to humans in strength. Observational data include the suspension of a two-week-old chimpanzee from a horizontal rod by a single arm for 5 minutes (Riesen and Kinder, 1952, p. 141; Edwards, 1963a), the ease with which older infants have produced bruises on humans to which they cling (Nissen, 1931, pp. 64-65; Hayes, 1951, pp. 42-43), and the fracture by "Mike," a 115-pound adult male chimpanzee, of a steel ring 5 inches across and formed from cyclindrical steel of 5/8-inch diameter, pulled by only two fingers (M. Manuel, personal communication, 1961).

Such anecdotal observations are indicative but very difficult to quantify, so more direct measures of chimpanzee muscular force should be far more satisfactory. Observation traditionally precedes and aids test design.

3. EXPERIMENTAL DESIGN CRITERIA FOR STRENGTH TESTING

All investigators are presumably cognizant of the basic principles of adequate scientific method in experimentation, including standardization of procedures, use of subjects in sufficient number, and recording of all likely relevant information. But in practice such ideals are not always followed.

Shortcomings in research methodology tend to be especially frequent in fields proportionately little studied, and that study by relatively few investigators. For example, experimentation on the effect of the proportion of maximum reach required of monkeys in the selection of the larger of two squares (Harlow, 1951, pp. 214-215) is among the very few studies of laboratory animals concerned with quantity of effort; most have been limited to primarily qualitative performance. Therefore, an unusually high frequency of procedural deficiencies might be anticipated in tests of chimpanzee strength.

For reasons explained in the introduction, the present writer first formulated the criteria for adequate strength testing listed in the present section and then searched the literature for discussions of such criteria. That a few of these criteria had received at least limited consideration was evident in the reports of Bauman and of Finch, to be considered in subsequent sections of this paper, but the prior consideration of even these few criteria was almost entirely no more than implicit. Finally, a few more explicitly formulated criteria were discovered in the much more developed field of human strength testing. Wilkie (1950, p. 250) lists geometrical simplicity of the joint, small number of muscles with small origin and insertion areas, non-disturbance of "rigid fixation" of body regions not involved in the muscular activity, and "accurately reproducible" movement requiring only slight skill. H. Clarke (1954, p. 137) adds the need for minimizing muscular fatigue by "systematically changing the sequence of tests for each testing period."

The writer suggests that perhaps as many as thirty-seven criteria are essential to obtain valid results in comparative strength testing of infra-human primates.

(1) Exclusion of the kinetic energy of the subject from the indicated force (Hubbard and Mathews, 1953, p. 43).

(2) Exclusion of the kinetic energy of the moving parts of the measuring device from the indicated force.

(3) Minimization of friction between force and its indicator.

(4) Precision of measurement in the overcoming-of-resistance method by using small increments to resisting force.

(5) Design of apparatus to permit control of relevant body segment angles.

(6) Approximately horizontal direction of applied muscular force.

(7) Satisfactory fit of apparatus to subject.

(8) Minimization of apparatus characteristics tending to induce distraction or even fright in subject (Bauman, 1923, p. 432).

(9) Essentially isometric condition of muscles (Ritchie, 1928, pp. 29-30).

(10) Brevity of muscular contractions in order to avoid complicating strength scores by variations in endurance (Hunsicker, 1957) -- permissible because of lack of noticeable effect on strength scores by rate of developing maximum tension (Ralston, et al., 1949, p. 531).

(11) Recognition of fatigue and estimation of its effect made possible by changing the sequence of muscles tested and comparing scores.

(12) Minimization of fatigue by adequate spacing of successive tests.

(13) Recognition of three distinct "maximum strength levels": maximum force exertable with injury-avoidance inhibition, maximum force without injury-avoidance inhibition under normal conditions, and maximum force under emergency (Barcroft and Konzett, 1949, pp. 201-203; Brown, Goffart, and Dias, 1950; Young, 1951, p. 94; Best and Taylor, 1955, pp. 827-837).

(14) Determination of which of the three horizons is represented by each score.

(15) Standardized positions of subjects (Cureton, 1947, pp. 363-365; Hugh-Jones, 1947).

(16) Bracing of significant portions of the body.

(17) Optimum muscle length for maximum force -- in most cases almost fully extended (ibid.) -- generally preferable (Haxton, 1944).

(18) Minimization of muscle elements contributing to external leverage strength (Edwards, 1963b).

(19) Standardized performance.

(20) Performance-training of chimpanzee subjects (Köhler, 1921) and performance-practice of human subjects (Cureton, 1947, p. 362; Hubbard and Mathews, 1953, p. 42), virtually essential for standardized performance.

(21) Immediate indication to subject of successful effort, for training and practice (Ruch, 1958, p. 331).

(22) Varied quantities and kinds of motivation to elicit equivalent response from highly individualistic chimpanzee subjects (Yerkes, 1943).[1]

(23) Utilization of positive motivations (Ruch, 1958, pp. 324-326), such as curiosity (though rapidly declining), hostility

(though inconsistent and even associated with varying strength horizon), ego-expression (though generally unreliable), imitation (Yerkes, 1943, pp. 133 and 142), the desire for affection and approval, including verbal praise, applause, pats on the head, and even an offer or permission to groom (Yerkes, 1943, pp. 50 and 138), and especially the generally stronger and more consistent "physiological drives" (Jersild, 1954, p. 835).

(24) Utilization of negative motivations, perhaps generally even more useful than positive motivations (Yerkes and Yerkes, 1929, p. 343), such as verbal disapproval, bluffed corporal punishment (Nissen, 1951, p. 450), corporal punishment, spray of water (Patton, 1951, p. 473), and other forms of punishment (Yerkes, 1943, p. 138).

(25) Utilization in training for strength testing of approximately the same moderate intensity of motivation found optimal for problem-solving (Birch, 1948; Ruch, 1958, pp. 326-327), but increased intensity of motivation for actual strength testing.

(26) Equivalent and preferably optimal[2] physical environment during all tests.

(27) Optimal state of health of the test subjects.

(28) Optimal muscle glycogen level in test subjects.[3]

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[1]Low variability of temporally well-separated scores reflects the effect of the upper limiting asymptote as the maximum in each strength level is approached (Edwards, 1963b). Therefore, despite much opinion to the contrary, as long as the testing remains within the same strength level for all scores of different subjects compared, any single motivation or combination of motivations is satisfactory if a subject's maximum scores on successive days manifest low variability, regardless of how different these motivations are from those producing the most consistent results with other subjects.

[2]Contrary to much naive assumption, optimal environment is not necessarily that in which the species is generally found in the natural habitat (Nissen, 1951, p. 428; Cole, 1957); furthermore, optimal environment varies according to the nature of the tests conducted.

[3]The average rate of reduction in glycogen concentration is likely greater in chimpanzees, adapted to large quantities of almost exclusively plant food of low caloric value at frequent intervals (Nissen, 1931, pp. 52-69), than in humans, most of whose evolutionary adaptation since earliest Pleistocene times has been associated with a largely carnivorous diet of smaller quantities of more concentrated food at much more sporadic and infrequent intervals.

(29) Fairly equivalent frequency, intensity, and duration of exercise in the life-history of compared subjects (unless intentional and accurate variation of exercise).

(30) As with humans (Hunsicker, 1955, p. 7; D. Clarke, 1960), retesting at different hours and different days to reveal a chimpanzee's consistency of strength and/or effort (Yerkes, 1943, p. 474).

(31) Recognition that validity of maximum test scores is confirmed by relatively little day-to-day variability.

(32) "Longitudinal" retesting to determine day-to-day and year-to-year intra-individual variability, preferably with intentional variation of as many determinants as possible, including age, size, exercise, nutrition, and, in mature females, phases within the sexual cycle.

(33) Adequate samples of subjects with body-size, age, sex, nutrition, and exercise essentially constant for the determination of approximate inter-individual variability due to other factors.

(34) Adequate samples of subjects with such factors as body-size, age, sex, nutrition, and exercise widely varied for correlations to ascertain the approximate influence of each determinant on muscular strength.

(35) Recording of the applicable and more significant measures of "panometry" (also termed "chimpometry") and anthropometry, for various correlations and estimates -- such as force per unit of cross-sectional muscle area -- and publication of these data for detailed comparisons and other potential uses in subsequent investigations.

(36) Recording and publication of the relevant life-history of each subject, for purposes comparable to those indicated for criterion 35.

(37) Recording and publication of as much additional possibly relevant data on the environment, the subject's condition, and the subject's performance as feasible, for purposes comparable to those indicated for criterion 35.

4. EXPERIMENTS BY BAUMAN

A. Methods

Apparently the first formal experimentation designed to measure chimpanzee strength was conducted by Bauman (1923; 1926) some four decades ago. Bauman's methodology will be very briefly considered in the same sequence as the requisite criteria in the preceding section of this paper.

A heavy rope attached to a dynamometer was passed through the bars of the chimpanzee's cage, where it was pulled by the subject, who grasped the wooden or rope-loop handle.

A standardized posture while performing the pull was attempted by providing sufficient length of rope for the chimpanzee to brace himself, apparently with his feet at the juncture of the bars and floor, and by instructing the human subjects to assume approximately the same position as the chimpanzees.

Motivations were apparently limited to hostile rage, to ego-heightening display of strength, and to curiosity.

Very little information is reported about the condition or life-histories of the subjects, but the two chimpanzees yielding likely significant results -- "Suzette," an adult female purportedly weighing some 135 pounds, and "Boma," an adult male estimated at 165 pounds -- were apparently healthy, of presumably unknown age, at least quantitatively well-nourished, but quite certainly having had relatively little exercise for some years.

Some attempts to retest subjects were made, but with very limited results because the animals "quickly lost interest in" the apparatus (1923, p. 432). Procurement of test scores on five chimpanzees (as well as four orangutans) was attempted. The reports of the experimentation are very brief and incomplete.

B. Results

When first exposed to the test apparatus, "Suzette" exhibited "malicious rage" and, seizing the rope in an evident attempt to break the device, scored a pull of 1260 pounds, despite considerable flexure of the legs at the knees (1923, p. 434). Almost a year later, with a "very deliberate" two-handed pull and "absence of particular effort," she scored 905 pounds (1926, p. 3). Other scores ranged from 100 to 580 pounds.

"Boma" was induced to pull a number of times, but his only high scores were 847 and 640 pounds, accomplished with his right arm only (1923, p. 437). The higher pull was scored with both feet braced on the floor and with the left hand grasping the door of the adjacent cage. The pulls quickly declined to 200-400 pounds. Months later, "both his previous fear and subsequent curiosity being completely lacking," not even light pulls were made (1926, p. 2).

Three other chimpanzees achieved only unimpressive scores.

Hand-grip dynamometer tests were conducted only on an adolescent 95-pound male orangutan, with scores up to 141 pounds for the right hand (1923, p. 438).

Seven 127- to 170-pound human males, most of them members of a college football team, were later tested with the same apparatus for two-handed pulls (1926, pp. 4-5). Quick two-handed pulls ranged from 369 to 428 pounds for six subjects, while slow two-handed scores were from 271 to 491 pounds for the same men. A pull at medium speed by the 127-pound seventh subject registered 460 pounds.

With the aid of the left arm, which grasped a fixed support in the fashion of "Boma," five of the seven human subjects exhibited right-handed pulls of 147-210 pounds.

Considering "the fast (and medium) pulls as most comparable," Bauman then converted the human two-handed scores by multiplying them by the ratio of chimpanzee to human body-weight. Based upon the converted pulls of 266-489 pounds, Bauman computed a ratio of chimpanzee strength superiority of 2.57:1 to 4.73:1. The same procedure applied to the five one-handed pulls yielded converted scores ranging from 177 to 220 pounds, and ratios of 3.85:1 to 4.78:1. Finally, by the average ratio of human two- to one-handed pulls, 2.26:1, Bauman calculated that "Boma" could have pulled 1914 pounds two-handed and was 1.52 times as strong as "Suzette" or 1.24 times as strong when converted "weight for weight" (1926, p. 7).

C. Evaluation

Point-by-point comparisons between the requisite criteria and Bauman's methodology show that only a very few of these thirty-seven criteria were adequately satisfied. The following observations will be limited primarily to the more significant and to those not necessarily apparent to the reader.

Methodological and analytical shortcomings include the following: probable dynamometer inaccuracy, in part due to kinetic energy effect; the likelihood that the limiting factor in the pulls was not leg, back, or arm strength but was either the limited hand-grip afforded or hand strength; the reflection of different strength horizons; highly variable subject position (for which no training is possible unless subjects can recognize "successful" pulls); inadequate, inconsistent, and transient motivations; fourteen errors in computed ratios (1926, pp. 5-6); the unsatisfactory nature of direct body-weight ratios, which penalize all humans and larger subjects of both species (Edwards, 1963b); and the closer comparability of "Suzette's" 905-pound two-handed pull than her pull of 1260 pounds in hostile rage (third horizon), with reduction in chimpanzee superiority in two-handed force to 1.85:1 to 3.40:1, although remaining at more than 4:1 for one-handed pulls.

Finally, although not analyzed or explicitly recognized by Bauman, evidently far more than a score of muscle components were significantly involved in the performances.

The two-handed pull, at least for chimpanzees, likely indicated leg extensor strength primarily. But the one-handed pull was very different; "Boma's" left arm flexors likely provided as much force as his leg extensors. By substituting "Suzette's" 905-pound pull for comparisons and reducing "Boma's" estimated two-handed pull from 1914 to 1210 pounds, the present writer would reduce the male chimpanzee's proportionate and relative superiority over the female from 1.52:1 and 1.24:1 to 1.34:1 and 1.09:1.

5. EXPERIMENTS BY FINCH

A. Methods

Two decades after the studies of Bauman, Finch (1943) attempted "to clarify and to supplement Bauman's data" by somewhat more sophisticated experiments at the Yale Laboratories of Primate Biology, Orange Park, Florida.

Weights (ten-pound disks of cast iron) were attached to a rope which passed around several pulleys, one of which was secured to a wooden block, to which a one-inch manila rope was also secured. In testing an ape's strength, the heavy rope was inserted through the bars and into the cage. Sufficient force applied to the manila rope resulted in the horizontal sliding of the block and the lifting of the weights, with a theoretical mechanical advantage of 0.5, but a variable actual advantage -- measured by connecting a spring-scale at the subject's end of the heavy rope and pulling it with a windlass -- of only 0.22-0.27. No form of rigid or rope-loop handle was provided.

Despite several days in which to become accustomed to the apparatus, the chimpanzees probably manifested posture only a little more standardized than in Bauman's experiments.

Fruit placed on the wooden block and procurable when the block was pulled in 9 to 12 inches provided apparently the only motivation. With augmentation of the incentive at one-minute intervals, the series was terminated after ten minutes if the block was not successfully moved (Finch, 1943, p. 225).

The chimpanzees were tested "in the morning before a major feeding" and then the following day after "24 hours prior food deprivation" (1943, p. 224).

Of the four adult male and four adult female chimpanzees tested, five were "among the healthiest and most vigorous animals in the colony; the other three ("Jack," "Pati," and "Cuba") were "in good condition" but not. . . especially vigorous and healthy" (1943, p. 224).

Four adult human males working at the laboratory were also tested. Presumably, there was no retesting after the two days indicated.

B. Results

The results of the experimentation are summarized in Table 1.

Table 1

Body-Weights and Pulls of Chimpanzee and Human Subjects
Tested by Finch (1943)

Subjects	Body-Weight (lbs.)	Maximum Pull		Ratios of Pull to Body-Weight	
		Normal (lbs.)	24-Hour Deprivation (lbs.)	Normal	24-Hour Deprivation
Male Chimpanzees					
Jack	122	450	450	3.7	3.7
Frank	108	450	413	4.2	3.8
Bokar	107	487	---*	4.6	---
Pan	106	375	413	3.5	3.9
Female Chimpanzees					
Mimi	109	227	264	2.1	2.4
Lita	103	300	375	2.9	3.6
Pati	103	227	194	2.2	1.9
Cuba	82	300	---*	3.7	---
Male Humans					
1	190	525		2.8	
2	145	487		3.4	
3	145	450		3.1	
4	135	338		2.5	

*Refused to pull

Ratios of maximum pull to body-weight averaged slightly greater for human males than those of the seven maxima of chimpanzee females (2.95

versus 2.69) and not too appreciably less than those of chimpanzee males (3.91). In absolute force, the humans outpulled even the male chimpanzees.

C. Evaluation

Clearly, Finch's methodology was more sophisticated than that of Bauman, but it is apparent that only a few of the thirty-seven criteria were adequately satisfied. For example, about half of the force applied to the rope was dissipated in friction, so the resulting variability of scores with constant force necessitates inaccuracy in computations of force. Spring-scales are also notoriously inaccurate, generally. The interval between successive minimum forces required to lift the weights was more than 30 pounds. The lack of a rigid or even rope-loop handle may have resulted in enormous reductions in exertable force.

The work expended in series of pulls likely reduced maximum force significantly, while changing muscle lengths could not have remained optimal or even comparable, for very little postural standardization is indicated.

The angle of the rope was presumably quite variable, and resulted in marked reductions in registered force.[4]

The single motivation relied upon seems inadequate, especially since its effectiveness became reduced with each rewarded success. The inconsistency of tests after food-deprivation (only three chimpanzees registered increased strength) was presumably due to the counteracting effects of two widely variable factors of roughly equivalent magnitude -- the appreciable enhancing of motivation opposed by the diminishing of strength and especially endurance resulting from marked decrease in tissue glycogen level.

The apparent lack of retesting of the chimpanzee (and human) subjects under approximately constant conditions constitutes a significant shortcoming. Apparently no attempt was made to record panometric and anthropometric data other than body-weight or to correlate such measures with maximum force. Very little information on the experimental results was reported.

6. EXPERIMENTS BY OTHERS

Yerkes apparently made occasional strength measurements on chimpanzees, but the only direct account which the writer has been able to

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[4] The effective force applied to the block was the product of the actual force applied to the rope and the cosine of the angle between the rope and the line perpendicular to the side of the block toward the cage.

locate pertains to his spring-balance tests of the young female gorilla "Congo"; for the positive motivation of food, at the age of four to five and weight of 65 pounds, pulling a rope with both hands and with her feet braced, she registered 160 pounds, and a year later at the weight of 128 pounds she pulled 240 pounds. Since these pulls were manifestly sub-maximal, it was concluded that the five- or six-year-old gorilla was at least two to three times as strong as an adult human (Yerkes, 1927).

Also employing food incentives, Morris has for some years been testing at regular intervals the strength of an immature chimpanzee at the London Zoo (J. Goodall, personal communication, 1962).

Finally, indirect strength tests have been conducted by Crawford (1937), who trained single young chimpanzees to pull by means of a rope a weighted box containing food. When the weight was increased, two chimpanzees learned only by "accident" to pull together, but soon a chimpanzee when hungry would successfully solicit his satiated partner to assist in pulling the box to their cage.

7. APPRAISAL OF CHIMPANZEE STRENGTH

A. Theoretical

One method of estimating chimpanzee strength is based upon theoretical and general considerations. To be meaningful, an evaluation of strength must be considered in relative rather than purely absolute terms. Both because of general experimental familiarity in tests of strength and because of "practical" value, man will be employed as the standard of comparison with the chimpanzee.

Even if there were no genetically determined differences in muscular ontogeny or physiology, under natural conditions chimpanzees use all major groups of muscles both intensively and extensively every day, so a marked superiority over most humans due to differences in exercise alone might be anticipated (Yerkes, 1943, p. 112). Only such rare humans in the modern world as migratory hunters would have fairly equivalent exercise, and even these humans have much less exercise of the upper limbs than climbing and brachiating apes.

Marked genetic differences between ape and man would be expected for several reasons. The basis for the first hominid adaptive radiation -- grassland-dwelling with erect posture -- greatly increased the range of tolerance for many muscles, especially those of the upper limbs; that is, selective pressures for maintaining equivalent strength declined. Furthermore, since the acquisition of extremely advantageous complex social tradition (culture), members of the genus <u>Homo</u> have experienced greatly reduced selective pressures to maintain optimum genes and gene frequencies. Thus in earlier, small populations of man, genetic drift away from the optimum occurred with greater frequency and degree, while the dynamic equilibrium between mutation pressure and the selective removal of individuals with defective genes has continued to shift further from the optimum as culture has become increasingly influential and "permissive." But the selective pressures, especially on musculature for locomotion and food procurement, have remained very high in apes.

Other factors promoting genetic differences are derived from differences in ape and human social organization and behavior. Chimpanzees are organized into migratory bands of 2 to 20 individuals each; 25 bands counted by Nissen (1931) contained 4 to 14 members each, with an average of 8.5. Generally, each band has only one adult male, with one or more adult females. The implied inter-male competition evidently occurs in part through direct struggles for dominance, in which muscular strength is a significant factor (Yerkes, 1943, pp. 47-49), which therefore affects reproductive rates and resulting selective pressures. Selection for the ability of the male to defend against predators acts somewhat similarly but at the group (family and deme) level. Selection for dominance and defense also operated on ancestral humans at both the individual and group level but with much reduced pressures both because of the generally probably increased male-to-female sex ratio[5] and because muscular strength progressively declined in significance as a determinant of dominative and defensive success. Struggles for dominance and defense against predators applied selective pressures primarily to males but also to a lesser extent to females; even if there were no dominance or defense pressures directly applicable to females, some of the genetic selection for stronger males would be transmitted to female offspring as well, since sexual dimorphism is not extreme in either chimpanzees or humans.

Through the operation of geometrical similitude, there is far less tolerance ("leeway") in chimpanzees than in monkeys of much smaller body-size between minimal muscle size for requisite strength and feasible muscle size, other factors considered. Therefore, with body-size, sex, and maturity constant, relatively little inter-individual variability would be anticipated in chimpanzee strength.

As a result of the foregoing considerations, it may be concluded that selective pressures for the maintenance of maximal feasible strength are greater in chimpanzees than in humans or monkeys. With body-size, sex, and maturity constant, chimpanzees should also have appreciably less inter-individual variability in strength for most groups of muscles than smaller monkeys or erect and culture-bearing humans, especially since muscular force is affected by upper limiting asymptotes (Edwards, 1963b).

The more frequent need in chimpanzees to summon near-maximal strength would be expected likely to result in a lowered sensitivity to pain. Thus

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[5] Very great emphasis on warfare and thus much higher male mortality rates apparently occurred only rarely among pre-neolithic populations.

chimpanzees should manifest a less distinct -- and therefore insignificant -- first level of strength than humans for those sets of muscles which in man are markedly affected by injury-avoidance inhibition.

The greater selective pressures operating on chimpanzees would be expected not only to have maintained the size and efficacy of most muscles but also, since emergency conditions crucial to survival occur more frequently to chimpanzees than to humans, the optimum ease of "firing" all or a higher percentage of muscle units should be greater in the ape. Therefore, theoretically anticipated would be a closer approximation of the chimpanzee second (normal) level of strength to the third (emergency) level.

The greater chimpanzee ease of approaching the second and third strength level maxima, presumably asymptotically, should result in less variability of valid maximum scores in successive series for a given chimpanzee subject than for a human, for whom average retest coefficients of correlation are typically .90 to .92 (Hunsicker, 1955; Clarke, 1960).

Finally, it may be observed that the freeing of the arms from any primary function in human locomotion and the development of culture with the need for more complex and precisely controlled movements of the hands and arms has resulted in a greater emphasis on handedness in man. It seems improbable that any significant hereditary superiority in potential muscular strength of one arm normally exists, but marked differences in use -- as Kellogg and subsequent researchers have shown -- affect the placement in the atrophy-hypertrophy continuum and thereby generally result in a moderate but decided inferiority of left (rarely right) arm strength, averaging approximately 10 per cent (Hunsicker, 1955). Because of varied manipulative functions, some handedness should be and reportedly is present in chimpanzees (Yerkes, 1943, pp. 113-114), but the average differences between precisely accurate contralateral scores of the chimpanzee brachium, antebrachium, or hand muscles should be decidedly less -- perhaps only one-half to one-third as great -- than the human differences in these scores.

B. Empirical

The other method of estimating chimpanzee strength is based upon observational data.

Other factors equivalent, strength is proportionate to cross-sectional muscle area. General observations of others that the proportionate size of most muscles, including virtually all of the upper limb musculature, is greater in the chimpanzee than in man has been confirmed by the writer's anatomical studies at the Aeromedical Research Laboratory of Holloman Air Force Base (1963e; 1963f). Other factors such as differences in leverage may also account for marked distinctions in manifested strength (Edwards, 1963c).

Such data as those concerning muscle size and leverage indicate the likelihood of marked variation in strength from one species to another, but only direct manifestations of strength can demonstrate that such differences definitely exist. Anecdotal observations seem to reveal superiority of chimpanzee strength over that of humans, but the shortcomings of such data are evident. Primary reliance should be placed upon experimental evidence.

The report of Finch (1943) and the general evaluations of Hooton (1942; 1946) and Yerkes (1946) seem to imply skepticism regarding the validity of Bauman's very high scores. But an appraisal of the two major series of chimpanzee strength tests, those of Bauman and of Finch, does not necessitate the invalidation of one series, or even a decided choice of one as more representative. If, because of the greater experience of Finch and his associates in studying and testing chimpanzees and because of the greater methodological sophistication of this more recent experimentation, it is concluded that Finch's data are valid, the many differences in test conditions could readily account for the apparently contradictory results.

Perhaps the most significant factor differentiating the scores procured by Finch from those of Bauman was the lack of any form of handle in Finch's apparatus; therefore, the "weakest link" for the apes tested by Finch was likely their strength in grasping the rope. Perhaps also of some significance was the possible inability of Finch's chimpanzees to adjust the length of rope and angle of pull as well as did the humans in Finch's experiments or Bauman for his chimpanzee subjects.

Likely even more important than the difference in form or mode of utilization of the apparatus as a factor accounting for the contrast in chimpanzee strength scores was that of motivation. As discussed, "Suzette's" highest score and quite possibly her subsequent 905-pound and "Boma's" 847-pound scores were apparently well within the third horizon of emergency strength. Contrastingly, Finch's apes, working for food incentives which had varying effectiveness -- as indicated by a marked variability between first (no food deprivation) and second (24-hour food deprivation) maxima -- were apparently scoring slightly to markedly below the maximum strength exertable in the second horizon of normal conditions.

It seems possible that the general health of the chimpanzees tested by Finch at the Yerkes Laboratories was not nearly so good as was deemed the case. Unlike "Suzette" and "Boma," relatively isolated in zoological gardens, the Florida apes, members of a large colony in a subtropical climate before much current knowledge of the causes of chimpanzee morbidity and its control had developed, lived under conditions almost ideally facilitating parasitism and the transmission of parasites.

Even though the body-weights of Bauman's chimapnzees were almost surely over-estimated, Finch's subjects were decidedly smaller and thus likely somewhat less mature. Since strength development is at least to some extent associated with maturity -- through intrinsic ontogenetic processes and the cumulative effects of additional years of exercise -- another likely factor in the reconciliation of the conflicting results is apparent. But "Suzette" and "Boma" may have been no more mature than their smaller cousins, and the maturity factor may be relatively insignificant in any event. Among the human subjects, Bauman's football players were almost surely in excellent physical condition, but the condition of most of Finch's laboratory workers was apparently at least almost equivalent.

Other factors noted in the foregoing discussions, such as the likely inclusion of kinetic energy in the maximum pull registered by "Suzette," may also have contributed to the marked differences between the scores obtained by Bauman and those by Finch.

8. SUMMARY AND CONCLUSIONS

It has long been recognized that differences in muscular strength may constitute the greatest distinction between man and his closest analogue, the chimpanzee, with the exception of the higher mental processes. If marked differences exist, these must first be determined before research on the factors involved in these differences -- crucial to an understanding of certain aspects of both the chimpanzee and man -- can be most effectively pursued.

Anecdotal observations indicate that, at least in times of stress, chimpanzees are much stronger than humans under normal conditions, but such observations are inadequate for an evaluation of relative strength under comparable extent of motivation or stress.

Some thirty-seven criteria are requisite for adequate strength testing of chimpanzees.

Bauman (1923; 1926) secured very high strength scores on one adult male and one adult female chimpanzee, with an apparent ratio of superiority to humans per unit of body-weight of approximately 2:1 to 3:1 for two-handed pulls by the entire body on a loop or rod handle with the legs flexed and braced. The ratio for the similarly positioned but very different one-handed pull was approximately 4:1.

Finch (1943), in more sophisticated experiments, procured two-handed per unit of body-weight ratios for pulling on a handleless rope averaging 1.33:1 for adult male and 0.91:1 for adult female chimpanzees when compared with adult male humans (calculated by the present writer).

Although the ratios obtained by Bauman and Finch are very inconsistent, the contrasting results are not necessarily due to any fundamental error in measuring or recording, and all reports are likely valid. Reconciliation can apparently be adequately achieved through consideration of likely differences in the subjects' condition and the marked differences in methodology. Especially significant are the effects of facilitation of grasp (handles) and the contrasting motivations employed. Even in the "deliberate" scores utilized by the present writer in computing the ratios for "Suzette" and "Boma," the maximum second level of strength was likely exceeded, while apparently the eight chimpanzees of Finch were inadequately motivated to reach that level.

It may thus very tentatively be concluded that, for those not very precisely identifiable muscles involved, chimpanzees are under comparable conditions very roughly two times as strong as humans in the two-handed pulls when a handle is provided and disproportionately stronger in the one-handed pulls described.

But neither Bauman, Finch, nor any other investigator has satisfied more than a few of the thirty-seven criteria considered; therefore, if a valid appraisal of chimpanzee strength and a comparison of such strength with that of other species is of importance, further research on this problem is urgently needed.

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